

scribed earlier, and supporting most of the ferns listed above, should be investigated as a likely habitat for this genus anywhere in the Hawaiian Islands.

From this summary it may be concluded that the habitat of *Diellia* is a transient one, both edaphically and biotically, which occurs constantly but sporadically, both in time and area, through the steep and dryer wooded gulches of the Hawaiian Islands. It may be surmised that the apparent rarity of the genus is due to the relatively small areas that such suitable environments occupy at any one time. The "disappearance" of the genus from some of its former localities may be due to the removal of disturbing influences which provided appropriate edaphic and biotic conditions. On the face of present evidence it does not follow that the genus is "on the verge of extinction." Because its habitat is transitory, it has probably always been rare and local! Further field research may even reveal that *Diellia Mannii* still exists somewhere in western Kauai.

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The Problem of Generic Segregates in the Form-Genus *Lycopodium*¹

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During the academic year of 1947-8, it was my privilege to work under the guidance of the late Mr. C. A. Weatherby as Harvard Research Associate and as a scholar of the John Simon Guggenheim Memorial Foundation. Those of us (nearly every North American Botanist) who have worked with or under Weatherby or who have at one time or another asked him for help or

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advice can readily appreciate the advantage that was mine. While working on *Lycopodium*, I was able at any time to discuss problems with him, or draw upon his astounding knowledge of the botanical literature, or have his opinion on unusual problems in nomenclature. That I considered him as a friend and myself as his disciple goes without saying.

The genus *Lycopodium*, described by Linnaeus, has been subjected to the repeated attempts of later authors to subdivide it into more manageable and homogeneous genera. The first attempt was by Bernhardt² who proposed two new segregate monotypic (in 1801) genera: *Tmesipteris* Bernhardt and *Bernhardia* Willdenow. Both new genera were immediately accepted, but *Bernhardia*, Willd., being a later homonym, was replaced by *Psilotum* Swartz in 1806.

In 1804, Palisot de Beauvois published in the *Magazin Encyclopédique* a paper entitled "Prodrome de l'Aéthéogamie" in which six more generic segregations were proposed. For the genus *Lycopodium*, in the modern sense, he set up two new genera: *Plananthus* Beauvois and *Lepidotis* Beauvois; and for *Selaginella*, in the modern sense, four new genera: *Diplostachium* Beauvois, *Gymnogynum* Beauvois, *Selaginella* Beauvois, and *Stachygynandrum* Beauvois. As for *Lycopodium* L., the name itself was discarded altogether. In the following year Beauvois published separately a paper entitled "Prodrome des Cinquième et Sixième Familles de l'Aéthéogamie," which comprised a reprint of the earlier paper plus a list of the transfers necessitated by the new genera.

The proposals of Beauvois were entirely ignored until thirty-three years later when A. Spring revived one of Beauvois' genera, the monotypic genus *Selaginella*, as

² Journ. für Bot. 1800²: 131-133. 1801.

the name for the largest part of what was then called *Lycopodium* L. For years Spring published abundantly on *Selaginella*, and, after the appearance of his monograph of the genus in 1850, this new segregate genus became universally accepted.

There were a few more attempts, mostly half-hearted ones, to set up new segregates for *Lycopodium*. In 1900, E. Pritzel published the subgenus *Urostachya* Pritzel,³ which was later raised to generic rank as *Urostachys* by W. Herter and accepted as such by H. Nessel in his monograph of *Lycopodium*, "Die Bärlappegewächse," published in 1939.

Herter's proposal failed, without any justification, to take into account the fact that *Urostachys* lacks the essential character of priority over many other previous names, especially *Plananthus* Beauvois. This and other defects, such as the lack of Latin descriptions, erratic bibliography, and unusable keys, greatly diminish the usefulness of Nessel's monumental monograph.

The advisability of separating further segregates from *Lycopodium* has been the subject of much of my work during the years 1947-1948, yet I have been up to now unable to reach a satisfactory decision. From the point of view of the phylogenist and the morphologist, *Lycopodium* L. should probably be divided. The reasons advanced are based almost wholly on the structure of the gametophyte. True, the gametophytes of most species of *Lycopodium* are still unknown, but those known fall into neat and fairly homogeneous groups and show a remarkably wide range of variation, from primitive types to the most highly specialized forms to be found in the ferns and fern allies. From the point of view of phylogeny, it is somewhat disturbing to see both primitive and highly specialized types of gametophytes within the genus *Lycopodium*.

³ In Engl. & Prantl, *Natür. Pflanzenfam.* 14: 563. 1900.

To the field and herbarium taxonomist, characters drawn from the gametophyte are highly impractical, to say the least. Few plant collectors have ever found gametophytes of *Lycopodium*, and such gametophytes are difficult to identify unless the possible species are few in number, are already well known, and may be growing in the vicinity. Not that gametophytes are extremely rare; to be sure, they are not as frequent as full-grown sporophytes, but they are extremely difficult to detect.

If the gametophyte of *Lycopodium* suggests a heterogeneous genus, the sporophytes are on the other hand strikingly similar in appearance. The only characters of possible generic value in the sporophyte of the present-day *Lycopodium* are: the shape of the sporophylls, the mode of growth, and the method of vegetative propagation—surely very weak characters on which to separate genera. From a practical point of view, the shape of the sporophyll is almost always observable in dried specimens, but the mode of growth is not always obvious and only rarely indicated on the labels.

Below is given a contrasted summary of the characters on which segregates of *Lycopodium* could be based.

I. GROUP OF L. SELAGO L.

HABIT: Terrestrial plants, erect at the tip, decumbent and rooting below; bulblets borne on reduced branches often present in this group, always absent in others; branching strictly isodichotomous, all branches being symmetrical and functionally alike. Growth is indefinite, innovations being present, with groups of sporophylls alternating with groups of leaves, one group of each being produced each growing season.

SPOROPHYLL: Much resembling the leaves in appearance, but usually slightly smaller, sessile or petiolulate, with the sporangium born near the base of the blade.

GAMETOPHYTE: Elongated, simple, entire or sometimes with two short branches, dorsiventral, flattened, with a distinct complete or incomplete rim; rhizoids scattered on the underside; antheridia and archegonia scattered on the upper surface within the rim;

epidermis fairly well differentiated and one-layered; fungal tissue multilayered and occupying the whole of the lower half of the tissue of the gametophyte. No further cell differentiation is present, except for a vaguely delimited and differentiated storage tissue of somewhat larger cells, located immediately above the fungal tissue.

II. GROUP OF *L. PHLEGMARIA* L.

HABIT: Epiphytes, tufted, loosely hanging; branching strictly isodichotomous, all branches being symmetrical and functionally alike. Growth is usually definite, and arrested after the production of the first group of sporophylls; then, innovations are absent and all the leaves are below the sporophylls. But growth is occasionally indefinite in some species and always indefinite in at least one species, in which case the sporophylls and leaves are in alternating groups, as in *L. Selago* group. New stems arise from the base of the old ones (and probably adventitiously).

SPOROPHYLL: Similar to the sporophyll in the *L. Selago* group, but in many species much smaller than the leaves, the strobiles thus often being distinct.

GAMETOPHYTE: Subterranean, cylindrical, abundantly ramified, not dorsiventral; rhizoids scattered; antheridia and archegonia scattered or in groups among the rhizoids; no internal differentiation of cells; fungal tissue superficial in small scattered patches and in no particular relation to the rhizoids.

III. GROUP OF *L. SAURURUS* LAMARCK

HABIT: Terrestrial, the stems tufted or single, stiffly erect; branching strictly isodichotomous and growth always definite (See group of *L. Phlegmaria*). The tufted habit results from the stems arising from the base of the old ones, as in group II; if the plants are single, branching is candelabiform in appearance.

SPOROPHYLL: Very similar to the leaves of the *L. Selago* group.

GAMETOPHYTE: Unknown to me, but presumably as in group II.

IV. GROUP OF *L. CERNUUM* L.

HABIT: Terrestrial; branching heterodichotomous. The erect portion of the plant simple or branched; if branched (*L. cernuum* L.), a main axis is present with only part of the branches strobiliferous and a lower branch arching over to root at the tip and produce a new erect axis; if simple, the strobiliferous axis is erect (*L. inundatum* L.) and arises from an axis appressed on the ground or arching over, rooting at tip and becoming underground for a short distance. Innovations are absent, each part of the

plant living less than a full year, the growth of erect portion being definite, of arching portion indefinite. The strobiles are sometimes indistinct, as in group I (*L. inundatum* L.), sometimes conspicuous and similar to those in groups V, VI, and VII (*L. cernuum* L., *L. carolinianum* L.); being usually sessile or borne on a pseudo-peduncle as in groups V and VI.

SPOROPHYLL: Peltate and inserted near the base on a short stipe; sporangium borne at the junction of the blade and stipe. The sporophylls are sometimes fused laterally (See group VII).

GAMETOPHYTE: Superficial and green, more or less conical, with tapered end pointing downwards, the truncate end bearing numerous lobes; fungal patches sometimes absent, but usually one or more on the tapered part of the gametophyte; rhizoids present only at the fungal areas; antheridia and archegonia located between the bases of the lobes. Internal differentiation of cells is limited in extent, the fungal tissue being one-layered and superficial; behind the fungal layer, a more or less distinct palisade layer is usually present; the innermost cells are often slightly larger; the rest of the cells, actually the greatest number, are small and undifferentiated.

V. GROUP OF *L. CLAVATUM* L.

HABIT: Terrestrial, with shallowly to deeply buried rhizome of indeterminate monopodial growth and numerous erect epigeous branches of determinate growth; growth of both rhizome and erect stem carrying through more than one season, innovations thus being present on both; strobiles always distinct, sessile or borne on a simple or branched pseudo-peduncle bearing sub-verticillate reduced leaves, this terminating the main axis, the lateral branchlets not being strobiliferous.

SPOROPHYLL: Peltate, as in group IV, and always sharply differentiated from the leaves in size, color, etc.

GAMETOPHYTE: Subterranean, short-conical to bilobed, with the pointed end pointing downwards and the flattened end uppermost; distinct rim present and continuous; rhizoids on the lower part only; antheridia in clusters on the upper side of the rim; archegonia scattered within the rim; no internal differentiation of cells, except for a well developed fungal layer on the underside.

VI. GROUP OF *L. COMPLANATUM* L.

HABIT: As in group V. Leaves always reduced and more or less fused to the branches and disposed in rows (usually four rows);

pseudo-peduncle always present, sometimes vestigial. Otherwise as in Group V.

SPOROPHYLL: As to group V.

GAMETOPHYTE: Subterranean, conical, constricted just below the capitate upper end, the lower end pointed; rhizoids scattered below the constriction, absent above; archegonia and antheridia densely grouped on the capitate end; no internal differentiation of the cells of the capitate end; cells of the tapered portion in four distinct layers—from outside inward: a usually multilayered epidermis, a multilayered fungal tissue, a unilayered palisade tissue and central storage tissue of slightly enlarged cells.

VII. GROUP OF *L. LATERALE* R. BROWN

HABIT: Terrestrial, stiffly erect, with underground system of undetermined nature; growth carried through many seasons, but determinate, innovations thus being present; strobiles distinct, borne on short lateral branches.

SPOROPHYLL: As in groups V, and VI, but fused laterally and free at both ends, the sporangia thus being inside a tubular structure. Over each sporangium there is a pore that may be opened or closed by the flexion of the tip of the corresponding sporophyll, the outline of which is still distinct.

GAMETOPHYTE: As in group IV.

Can the splitting of *Lycopodium* into smaller genera be justified from the above? I am in doubt. Certainly the variations encountered in the *gametophyte* are major variations. But variations of the *sporophyte* are decidedly of a minor nature; they provide no sharp divisions and could not by themselves justify splitting *Lycopodium*. Worse, they are poor characters from the taxonomist's point of view, since so much of the identification work is done on dried material and important characters such as habit and mode of growth are often impossible to detect in dried specimens.

This much can be said: as far as they are known at present, the gametophytes fall into five distinct types associated with the various types of sporophyte in the following manner:

GAMETOPHYTE

SPOROPHYTE

Type A. Dorsiventral	Group I.
Type B. Ramified	Group II (and III?).
Type C. Lobed and green	Group IV and VII.
Type D. Conical and rimmed	Group V.
Type E. Highly differentiated tissues	Group VI.

Groups IV and VII have a distinct affinity. Besides similar gametophytes, both also have the sporophylls fused into a cylindrical tube in at least some of their species. Groups III seems to be nothing but species of group II that have adapted themselves to the terrestrial habit by becoming erect and rigid. Species with type C gametophyte (lobed and green) show the greatest diversity of the types of sporophytes: from weakly differentiated sporophylls to fused sporophylls or a distinct strobile born laterally or on a pseudo-peduncle; from leaves all similar, dispersed around the stem, to leaves in one plane and in dissimilar rows; from an aerial vegetative shoot to pseudo-bulbs or an underground system; from definite growth to indefinite growth and innovations. In contrast to species of type C, the types of sporophytes are decidedly similar in habit, appearance, and mode of growth in the species within each of the other types.

The gametophytes of only a fraction of the species of *Lycopodium* have been studied. How would the present subdivisions stand if gametophytes of most or all species were known? We do not know.

Even though genera are undoubtedly artificial units, they should offer two characteristics: (a) from a theoretical point of view, genera should be groups of closely related species, and should be differentiated from each other by basic structural differences; (b) from a practical point of view, genera should be easily recognizable groups, in such a way that once a number of species of a group are known, most other species will at once be rec-

ognized as members of the same genus, although the species themselves may be unknown.

Lycopodium, as it stands at present, lacks the first characteristic, but possesses the second to a superlative degree. If *Lycopodium* L. were split into four to seven groups, the resulting genera would probably show the first characteristic, but would they also have the second and more practical one? To this question, I cannot at present answer yes or no.

A key to the major divisions of *Lycopodium* L., if based on characters drawn from the sporophyte only, would be made up of subdivisions such as the following:

- A. Sporophylls sessile or petiolulate, not peltate; branching isodichotomous.
- B. Epiphytes Group II.
- BB. Terrestrials Groups I, III.
- or
- B. New stems arising from the base of the old ones or lacking Groups II, III.
- BB. New individuals resulting from the separation of successive branches due to the disintegration of the older parts of each plant, or new individuals sometimes arising from bulblets Group I.
- AA. Sporophylls slightly prolonged downwards at the base of the blade, thus peltate and stipitate; branching heterodichotomous.
- C. No elongate monopodial vegetative shoot living a few years, all parts of the plant disintegrating within a year; innovations absent Group IV.
- CC. Elongate, monopodial vegetative shoot present and usually functioning as a rhizome, all parts of the plant remaining functional for a few years; innovations present Groups V, VI.
- or
- C. Strobiles borne laterally on short branches Group VII.
- CC. Strobiles borne at the end of erect axes or of normally developed branches. Pseudopeduncle often present. Groups V, VI.
- or
- C. Leaves free of the stem and branches, usually 6- or 8-farious Group V.
- CC. Leaves partly adnate to the branches, usually 4-farious. Group VI.

Because of the similarity of the problems involved, the development of the nomenclature of *Lycopodium* parallels the mosses. As pointed out by W. C. Steere,⁴ the Linnean *Hypnum* and *Bryum* were essentially form-genera. This was also true of *Lycopodium* in the Linnean sense and is still quite possibly true even in the modern sense. The natural classification of the mosses began to take shape when Hedwig started stressing the importance of the reproductive structures, mainly the peristoma. Similarly, we now consider *Tmesipteris*, *Psilotum*, *Lycopodium*, and *Selaginella* as widely separated genera on the basis of the characters of their spores and sporangia, but we are unable to make full use of the characters of all the reproductive structures because the prothallia of only a minority of the species are known and because the sporophyte is almost never associated with the gametophyte, thus rendering impractical any classification based on the gametophyte.

There is, in the present state of our knowledge, a good possibility that groups based on the characters of the prothallia might be natural groups and that it might be possible to define those groups in terms of the characters of the sporophyte. This possibility, if confirmed, would naturally lead to the splitting of *Lycopodium* in its current sense and the setting up of 4 to 7 segregate genera. However, such a step should not be taken until the gametophytes have become known for at least a majority of the species of each group concerned. Not enough is known yet of these gametophytes to justify such generic segregation, while, on the other hand, the groups listed above are based on minor vegetative characters that do not suffice in themselves for the splitting of the genus *Lycopodium* L.

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⁴ Bryologist 50: 251. 1947.